DISJUNCTIONS IN HOMOSPOROUS VASCULAR PLANTS[1]

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Pteridophyte geography has been examined from a number of standpoints (*cf.* Christ, 1910; Winkler, 1938; Tryon, 1969, 1970). A complete assessment of the significance of their geographical disjunctions would be difficult to make because of the numerous factors involved. The following discussion will concentrate upon special problems and the examples will have a strongly North American bias. Homosporous vascular plants are pteridophytes which lack micro-megaspore differentiation; all of the spores are presumably bipotential and capable of producing gametophytes with both sex organs. These pteridophytes include some of the widest ranging of all vascular plants, such as *Lycopodium clavatum, Osmunda regalis, Cystopteris fragilis*, and *Asplenium trichomanes*. The distribution patterns of pteridophytes in general are basically like those of seed plants: Narrow endemism is common, and long distance disjunctions frequently occur. One of our major concerns is whether a given disjunction may not be the result of a casual spore introduction. As Klekowski (this symposium) has pointed out, there are significant contrasts between ferns and seed plants, not only in means of dispersal but in their genetic apparatus as well. Some patterns of distribution, *e.g.* eastern Asia–North America and the amphitropical ones, may be related to major events in earth history. Others may be merely recent occurrences resulting from chance spores that traveled long distances.

Their popularity with researchers and field botanists has caused the pteridophytes to be well collected and represented in herbaria. In the eastern United States, for example, we know the ranges of these plants so well that finding a disjunct population only 100 miles from previously known stations is considered an event. As to what we may call a disjunction, there is, of course, no set definition. As Erickson (1945) showed in a species of *Clematis*, the range is made up of thousands of spatially separated populations. Ehrlich and Raven (1969) assert that distances of only a few miles or less may suffice to isolate plant populations from gene flow. Here I give as examples of disjunctions separations in range of as little as 100 miles.

Most of my examples (Table 1) deal with situations in which there is a large center of population and a small strongly disconnected population or group of populations. The principal seat or center will here be designated the "*metropolis*" and the small disjunct stand the "*outlier*." Although the metropolis was not necessarily the ancestral area, in some cases it probably was. Some taxa, as we go away from their centers of abundance, simply "fade out," their occurrences becoming

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more and more scattered, but lacking extreme peripheral disjunctions. The best example of transition from common to rare or sporadic in eastern United States is probably among the species of woodferns, *Dryopteris*, *e.g.* Crested woodfern, *D. cristata*; Spinulose woodfern, *D. spinulosa*, as we proceed down the Appalachian mountain chain. Common in the north, frequent in the middle range, and rare in the south, these species probably have no large gaps of 100 or more miles. Really large gaps are expectedly much more common in the western mountains because of their more xeric conditions and their more precipitous and isolated peaks.

The eastern North American–eastern Asiatic pattern of disjunction, first promulgated by Asa Gray, is illustrated by such examples as Shining clubmoss, *Lycopodium lucidulum*; the "Japanese grapefern," *Botrychium ternatum* (but see below); Interrupted fern, *Osmunda claytoniana*; and Sensitive fern, *Onoclea sensibilis*—all of which appear in more or less identical form in the eastern parts of the two continents (*cf.* Broun, 1938; Fernald, 1950; Wherry, 1961). Amphitropical distributions have been discussed by Raven (1963), who lists several pteridophytes. Probably the best example involving western North America and southern South America is *Polystichum mohrioides* (syn. *P. lemmonii;* also confused with *P.* × *scopulinum*; see Taylor, 1970: 172–187). The plants from Washington, Oregon, and northern California are closely similar to those from the Andes of South America and certain of the antarctic islands, and they are evidently conspecific.

An apparent near relative of the circumboreal and familiar Moonwort fern, *Botrychium lunaria*, is also amphitropical. The plant in question, which ranges from Los Angeles Co., California, far to the north in British Columbia and Alberta, is evidently the same as the species distinguished by A. H. G. Alston as *B. dusenii*, heretofore known only from Argentina (*cf.* Alston, 1960; Wagner & Lord, 1956). In at least some North American localities, *B. dusenii* grows sympatrically with *B. lunaria* (*e.g.* Snohomish Co., Washington). Probably all of the plants from western North America which were formerly identified as *B. minganense* are actually *B. dusenii.*

Although there is much interest in disjunctions of pteridophytes over water (*e.g.* Hawaii, Fiji, Samoa, Canary Islands, Galapagos—*cf.* Tryon, 1970), overland disjunctions across continents are equally intriguing, and they present different problems. Many intracontinental disjunctions are vexing because of seemingly suitable habitats in intervening areas where one would expect to find the plants in question. Oceanic disjunctions cause no problems from this standpoint because pteridophytes cannot grow upon the high seas or on intervening wind-swept atolls. Disjunctions of continental nature call forth all of the profound mysteries of plant distribution conjured up by the familiar phrase "rare and local."

SOME MAJOR DISJUNCTIVE TRENDS

In Table 1, I have listed a number of disjunctive "trends" in North American pteridophytes, giving the metropolis, estimated distance of the disjunction, ploidal level, and references. The following discussion refers to that table.

A. *North to South Trend.* In this the southernmost occurrences become widely separated, either "fading out" as they go southward, finally appearing only on the highest peaks, or forming more or less large disjunctions. Climate seems to be the major controlling factor, but often a given species is found upon one peak and then skips a number of others that would seem to be appropriate. When this happens we get disjunctions like those in Table 1. The Slender rock brake, *Cryptogramma stelleri*, was known only as far south as the ravines of northern Pennsylvania until Wherry (1961) found it in West Virginia: "Unexpectedly, there in a crevice so sheltered that the sun's rays never entered, and kept cool by evaporating moisture, was a colony of this tiny rock fern; its known range was thus extended some 200 miles southward."

The most peculiar north-south pattern is that of American Hart's-tongue, *Phyllitis scolopendrium* var. *americanum.* This fern has a strongly disrupted range except on the Niagara Escarpment of Bruce and Grey counties in Ontario (Soper, 1954), the center of its metropolis. All other stations are much further separated, and especially those far to the south in Tennessee. As early as 1878, Hart's-tongue plants were encountered in cool, damp limesinks there (Shaver, 1954). (The Mexican and Caribbean plants assigned to this species apparently represent a distinct subspecies.)

In connection with investigations of the spontaneous floras of pine plantations, a curious north-south disjunction was recently discovered involving the Braun's holly fern, *Polystichum braunii.* The "Marshall Tract" near the town of Ann Arbor, Michigan, was planted with species of spruce and pine on an old pasture during the 1920's and since, as in practically all similar plantations of the region, a distinctive, though small, spontaneous flora has arisen, including Running pine, *Lycopodium flabelliforme*; Spinulose woodfern, *Dryopterus spinulosa*; Sensitive fern, *Onoclea sensibilis*; and Ebony spleenwort, *Asplenium platyneuron.* A solitary plant of Braun's holly fern was discovered here in June, 1971, by Florence S. Wagner, growing in a deeply shaded valley with the foregoing pteridophytes. This constitutes a range extension of over 200 miles from the nearest locality to the north on South Manitou Island.

Hagenah (1955: 75–76) reported a disjunction of the sterile woodfern hybrid, *Dryopteris filix-mas* × *marginalis* in southern Lower Michigan—a single collection, some 200 miles south of the nearest localities to the north. Perhaps, in this case, certain "sterile" hybrids are able to produce occasional viable spores (Morzenti, 1967). Such spores are unreduced and capable of forming apogamous sporophytes.

Another example in Michigan which fits this pattern is the Mingan moonwort, *Botrychium minganense*, which I discovered south of Detroit in 1962. Commenting on this occurrence, Hagenah (1966: 159) wrote as follows: "The most unusual locality for this species in Michigan is that in Wayne County . . . far to the south of all other stations. Although only one plant was found here originally, it was observed for several years and now there are two." Since 1966 both plants, probably offsets of the same one, have disappeared. It probably represents an unsuccessful single spore introduction, the site being too far south for continued survival.

B. *South to North Trend.* Examples in which the metropolis is southern rather than northern are very few in homosporous pteridophytes. A prominent south-

TABLE 1. Some examples of outlying North American over-land pteridophytic disjunctions with rough estimates of mileages away from their metropolises. * = polyploid (level given if known). † = outliers suspected of being casual spore establishments rather than relicts of past floras.

	TAXON	METROPOLIS	ESTIMATED DISJUNCTION	PLOIDY	OUTLIER & REFERENCE
		A. NORTH TO SOUTH TREND			
	Botrychium multifidum	n. N. Amer.	100 mi.	2x	Madison Co., Va. (Wagner, 1946)
	Woodsia ilvensis	n. N. Amer.	100	2x	Ashe Co., N.C. (Bozeman, 1968)
	Botrychium lanceolatum var. *angustisegmentum*	n. e. N. Amer.	150	2x	Macon Co., N.C. (Wagner *et al.*, 1970)
	Gymnocarpium dryopteris	n. N. Amer.	150	4x*	Ashe Co., N.C. (Bozeman, 1968)
	Thelypteris phegopteris	n. N. Amer.	150	3x*	Macon Co., N.C. (Wagner *et al.*, 1970)
	Botrychium simplex	n. N. Amer.	200	2x	Giles Co., Va. (Wagner, 1963)
	Cryptogramma stelleri	n. N. Amer.	200	2x	Pendleton Co., W. Va. (Wherry, 1939)
†	*Dryopteris filix-mas* × *marginalis*	n. e. N. Amer.	200	3x*	Barry Co., Mich. (Hagenah, 1955)
†	*Polystichum braunii* var. *purshii*	n. N. Amer.	200	4x*	Washtenaw Co., Mich. (Wagner, unpubl.)
	Botrychium minganense	n. e. N. Amer.	200	4x*	Wayne Co., Mich. (Hagenah, 1966)
	Polystichum × *scopulinum*	n. w. N. Amer.	450	4x*	Cochise Co., Ariz. (Wagner, unpubl.)
	Phyllitis scolopendrium var. *americanum*	Bruce Peninsula, Ontario	650	4x*	Marion Co., Tenn. (Shaver, 1954; Fernald, 1935)
		B. SOUTH TO NORTH TREND			
	Ophioglossum vulgatum "var. *pycnostichum*"	s. e. U.S.	100	*	Lenawee Co., Mich. (Wagner, 1971)
†	*Dennstaedtia punctilobula*	s. e. U.S.	150	2x	Jackson, Shiawassee Cos., Mich. (Wagner, unpubl.)
†	*Adiantum capillus-veneris*	s. U.S.	700	2x, 4x	Fairmont, B.C. (Taylor, 1970)
		C. TREND TO SOUTHWESTERN MICHIGAN			
†	*Lygodium palmatum*	s. e. U.S.	300	2x	Kalamazoo Co., Mich. (Pippen, 1966)
†	*Woodwardia areolata*	s. e. U.S.	300	2x	Van Buren Co., Mich. (Billington, 1952)
	Dryopteris × *celsa*	s. e. U.S.	400	4x*	Kalamazoo Co., Mich. (Wagner *et al.*, 1969)
	Lycopodium appressum	e. Coastal Plain	600	2x?	Van Buren Co., Mich. (Wagner & Hagenah, unpubl.)
		D. TREND TO "DRIFTLESS AREA"			
	Asplenium × *pinnatifidum*	s. highlands	300	4x*	Iowa Co., Wisc. (H. Iltis, pers. comm.)
	Lycopodium porophilum	s. highlands	350	*	Grant Co., Wisc. (Hartley, 1966)
	Thelypteris simulata	e. Coastal Plain	700	4x*	Jackson Co., Wisc. (Hartley, 1965)

TABLE 1. (*Continued*)

	Taxon	Metropolis	Estimated Disjunction	Ploidy	Outlier & Reference
	E. East to West Trend				
	Cystopteris bulbifera	n. e. N. Amer.	650	2x	Guadalupe Mts., N. Mex. (Blasdell, 1963)
	Ophioglossum vulgatum "var. *pseudopodum*"	n. e. N. Amer.	1300	*	Kittatas Co., Wash. (Taylor, 1970)
	F. West to East Trend				
†	*Cystopteris* × *tennesseensis*	Cumberland Plateau	400	4x*	Jones, Craig Cos., N.C. (Wagner, 1965)
†	*Polystichum munitum*	w. N. Amer.	550	2x	Pennington Co., S.D. (Brooks, 1968)
†	*Gymnocarpium* × *heterosporum*	Lake Superior	650	3x*	Blair Co., Pa. (Wagner, 1965)
†	*Cryptogramma crispa* var. *acrostichoides*	w. N. Amer.	900	2x	Isle Royale, Mich. (Soper, 1963; Fernald, 1950)
†	*Cheilanthes castanea*	w. N. Amer.	1000	3x*	Montgomery Co., Va.; additional localities in Va., W. Va. (Knobloch & Lellinger, 1969)
†	*Pellaea* × *wrightiana*	s. w. N. Amer.	1000	4x*	Alexander Co., N.C. (Wagner, 1965)
†	*Asplenium septentrionale*	w. N. Amer.	1200	4x*	Monroe Co., W. Va. (Emory, 1971)
†	*Aspidotis densa*	w. N. Amer.	2200	2x	Megantic Co., Quebec (Fernald, 1950)
†	*Polystichum* × *scopulinum*	n. w. N. Amer.	2400	4x*	Gaspé Co., Quebec (Fernald, 1950)
	G. Sporophyte to Gametophyte Trend (Outliers all or mostly gametophytes)				
	Vittaria sp.	Tropics	250	?	Rabun Co., Ga. (Farrar, 1971)
†	*Grammitis nimbata*	Cuba, Jamaica	800	?	Macon Co., N.C. (Farrar, 1971)
†	*Hymenophyllum wrightii*	S. Japan	4500	?	Queen Charlotte I., B.C., Biorka I., Alaska (Taylor, 1970)

north disjunction is that of Southern maidenhair fern, *Adiantum capillus-veneris*, growing in Fairmont, British Columbia (Taylor, 1970), many hundreds of miles north of its normal latitudinal limit. This south-temperate to subtropical fern is flourishing in the runnels of a system of hot springs, an obviously unusual site.

Limitations of north extensions of many species into the Great Lakes area are probably due to cold winters and short growing seasons. Hay-scented fern, *Dennstaedtia punctilobula*, of the southern and eastern United States has been taken in Michigan on only two occasions, these widely separated in time. (A third collection, allegedly from the Keweenaw Peninsula of the Upper Peninsula, by O. A. Farwell, is under question.) In 1889, G. H. Hicks recorded a collection from Shiawassee Co. (specimen in University of Michigan Herbarium), and in 1954 I discovered it in Jackson Co. Of special interest for our subject is the fact that the latter collection comprised two juvenile plants, probably offsets from a single plant, found growing in the depression made by the overturning of a large tree—a transient habitat ideal for the growth of fern prothallia. In the loose, exposed sand there we found hundreds of gametophytes and young sporophytes of other fern species. One of the offsets of the Hay-scented fern was left *in situ*, but was gone the following year, having failed to survive the winter.

Our best example of "fading out" of species going northward is Ebony spleenwort, *Asplenium platyneuron*. Among the most abundant of ferns in southern and eastern United States, it decreases rapidly in numbers north of the Wisconsin glaciation in Ohio, Indiana, and Illinois (well illustrated in the last state by Mohlenbrock, 1967: 157). By the time we reach Michigan and Wisconsin, the plant becomes very sporadic. Some "colonies" are but a single plant. Of 21 counties in which Ebony spleenwort has been found in Michigan, only two are north of Saginaw Co. It was taken once at the University of Michigan Biological Station, Cheboygan Co., and has been found twice in crevices of limestone "pavements" in Chippewa Co. The suggestion seems plausible that this fern may be constantly re-established from wind-blown spores coming from the south. Single plants or small colonies may survive for a while and then perish.

C. *Eastern U. S. to Southwestern Michigan Trend.* In the Upper Great Lakes area, two regions have special interest for their pteridophytic disjunctions, the area along the southeastern shores of Lake Michigan and the "Driftless Area" of Wisconsin. The former is the region involving the counties of three states running from approximately Chicago, Illinois, to Muskegon, Michigan. From the standpoint of plant geography, this locality is famous for the most spectacular disjunction in the United States—*Thismia americana* (Burmanniaceae) which once grew near Lake Calumet, Illinois, separated from its nearest relatives in New Zealand and Tasmania (Swink, 1969: 411).

Of disjunct pteridophytes, several have been detected only during the past few years, *viz.* American climbing fern, *Lygodium palmatum*; the Log fern, *Dryopteris* × *celsa*; and the Southern clubmoss, *Lycopodium appressum*. All are at least several hundred miles from their metropolises. The clubmoss has only recently been distinguished, because it grows together with the closely similar Bog clubmoss, *Lycopodium inundatum*, with which it is readily confused.

D. *Eastern U. S. to "Driftless Area" Trend.* This well known focus of phytogeographical interest boasts three outstanding examples of pteridophyte disjuncts, namely the Massachusetts fern, *Thelypteris simulata*, a plant of low, sandy woods (Hartley, 1965); the Rock clubmoss, *Lycopodium porophilum* (also known as *L. selago* var. *patens*, but probably not the same; *cf.* Hartley, 1966; Wherry, 1961); and Lobed spleenwort, *Asplenium* × *pinnatifidum* (Iltis, personal communication)—both of the latter plants of sandstone cliffs.

E. *East to West Trend.* Very few pteridophytes show this pattern, in which the outliers are western. Most species which occur in both the East and West tend to skip the Great Plains and are actually "bimetropolitan" in that the eastern and western populations are more or less equivalent, neither being obviously the outlier of the other. Of bimetropolitan taxa I include such plants as Leather grapefern, *Botrychium multifidum*; Moonwort, *B. lunaria*; Least moonwort, *B. simplex*; Five-fingers or "American" maidenhair, *Adiantum pedatum*; Fragile fern, *Cystopteris fragilis*; Crested fern, *Dryopteris cristata*; Spinulosa woodfern, *D. spinulosa*; Spreading woodfern, *D. assimilis*; and Maidenhair spleenwort, *Asplenium trichomanes*. Some of these are undoubtedly connected in the forested areas at the north of the Great Plains. All of them are wide-ranging and are known also in Europe and (or) Asia. They are probably disjunctive due to past historical events.

Two examples which seem clearly to involve a metropolis in the East with outliers in the West may be cited. One is the Northern Adder's-tongue, *Ophioglossum vulgatum* var. *pseudopodum*, which is a frequent and widespread plant north of the line of maximum Wisconsin glaciation from the eastern coast (New Jersey to Quebec and Nova Scotia) west to Minnesota and western Ontario. This Adder's-tongue reappears in the Northwest, where it is exceedingly rare and local. Although it is possible that the western plants may represent a distinct variety, I doubt it. A second example, the familiar eastern Bulblet fern, *Cystopteris bulbifera*, occurs in a few very widely scattered localities in southwestern United States, the outlying stations hundreds of miles from each other. Bulblet fern is enabled to produce enormous colonies by forming gemmae, subspherical structures, along the costae, which abscise and roll, and will germinate into new sporophytes if they reach suitable sites. The Adder's-tongue, on the other hand, forms extensive colonies by root proliferation. Thus both of these plants are capable of developing large stands without sexual processes.

F. *West to East Trend.* In terms of number of examples and distances, this pattern of metropolis to outlier is the most striking of the directional trends. Some reach 2,000 or more miles in length of disjunction. Over half of those listed in Table 1 have been recognized only during the past 20 years, the outliers being so rare and local that they were overlooked. Wright's cliffbrake, *Pellaea* × *wrightiana*, is known from a single granite outcrop in North Carolina. The solitary locality in Pennsylvania for the Hybrid oakfern, *Gymnocarpium* × *heterosporum*, no longer supports a population, the limestone upon which it grew being now destroyed in the excavation of a quarry. The Forked spleenwort, *Asplenium septentrionale*, is so far represented in the eastern United States on only two rock cliffs in Virginia one-fifth of a mile apart. In view of the present incidence of populations in the outlying eastern region of these and others of those listed, the conclusion seems inescapable that at least some of them may not represent relicts of former floras in which the taxa were once more abundant and widespread. Rather they have arisen by long-distance spore dispersal following the prevalent winds from the west. Alternatively, some may have originated from spores on nursery or garden stock transferred from one part of the country to another, or escapes of western plants cultivated in the east.

G. *Sporophyte to Gametophyte Trend.* Surely the strangest disjunctions of homosporous vascular plants are those ferns that show dominant sporophytes in the metropolis and dominant gametophytes in the outliers. All of the examples discovered thus far are from North America (Wagner & Sharp, 1964; Farrar, 1967; Taylor, 1967), but we may expect additional examples to turn up in other parts of the world, especially in temperate rock outcropping regions. The examples involve tropical rainforest fern genera with gemmiferous gametophytes capable of dispersal by few-celled bodies which abscise and germinate, if deposited in appropriate sites. The gametophytes exist as disjuncts far into temperate latitudes, but their sporophytes form sporadically if at all, according to the researches of Farrar at Iowa State University (personal communication) involving examples of several groups of Filmy-ferns (Hymenophyllaceae), Shoestring ferns (Vittarioideae), and Dwarf polypodies (Grammitidoideae). In the wild these gametophytes are almost totally overlooked by vascular plant field botanists. Even bryologists, assuming presumably that the plants were algae, tended to disregard them in the past. Phycologists, upon encountering them, probably treated them as bryophytes. In view of our present knowledge, field botanists of all persuasions are urged to look out for these "ferns without sporophytes." They differ from "standard" cordate fern prothallia in being narrower and more profusely branched. Some are mere branching filaments. All produce more or less specialized gemmae, and even if they form tiny sporophytes, they usually do not complete the alternation of generations. The classical generalization that homosporous pteridophytes have dominance of the sporophyte generation does not apply in the outlying populations, and the plants behave more or less as do algae or bryophytes, occupying similar microhabitats on shaded cliffs and on damp tree bark. In the outlying populations the gametophytes no longer seem to "need" their sporophytes and spores, being able to propagate and spread entirely by their gametophytic gemmae.

H. *Indigenous to Naturalized Trend.* More and more pteridophytic disjunctions are being reported in which the populations of the metropolis are indigenous members of the flora and the outlying populations have resulted from man's activities. Two illustrative areas of such disjunctions in the United States are given in Table 2 listing the suspected artificial introductions in the states of Florida and Hawaii. Some of the taxa included, *e.g.* Ladder brake, *Pteris vittata*; and so-called "Garden maidenhair fern," *Adiantum hispidulum*, are now being naturalized in many places from cultivated garden and greenhouse plants. Some are conservatory and hothouse weeds. In some cases the same species may be both native and naturalized.

TABLE 2. Artificial pteridophyte outliers in Florida and Hawaii. Species listed in parentheses probably native in that state. Metropolises: O = Old World tropics, N = New World tropics, X = Pantropics.

	FLORIDA[a]	HAWAII	METROPOLIS
SELAGINELLACEAE		*Selaginella krausiana*	O
OPHIOGLOSSACEAE	*Ophioglossum petiolatum* (May be introduced in part.)	*O. petiolatum* (May be introduced in part.)	X
MARATTIACEAE		*Angiopteris evecta*	(?)O
POLYPODIACEAE	*Phymatodes scolopendria*	*P. scolopendria*	O
	(*Phlebodium aureum.*)	*P. aureum*	N
SCHIZAEACEAE	*Lygodium japonicum*	*L. japonicum*	O
	L. scandens (syn. *L. microphyllum.*)		O
ADIANTACEAE	*Adiantum hispidulum*	*A. hispidulum*	O
	Pellaea viridis (Volunteer in orchid houses.)	*P. viridis*	O
	Pityrogramma calomelanos (Probably introduced.)	*P. calomelanos*	N
	Pteris cretica	(*P. cretica*)	X
	P. ensiformis		O
	P. multifida		O
	P. vittata	*P. vittata*	O
	P. tripartita		O
		Ceratopteris thalictroides	O
ASPLENIACEAE	*Athyrium esculentum* (In and near gardens.)	*A. esculentum* (In and near gardens?)	O
	A. japonicum	*A. japonicum*	O
	Cyrtomium falcatum	*C. falcatum*	O
	Thelypteris torresiana	*T. torresiana*	O
	T. dentata	*T. dentata*	O
		T. parasitica	O
	(*Blechnum occidentale*)	*B. occidentale*	N
	Nephrolepis hirsutula (s.l.)	*N. hirsutula* (s.l.)	O
	N. cordifolia (Introduced in part?)	*N. cordifolia* (Introduced in part.)	X
		N. biserrata cv. "Furcans"	?
AZOLLACEAE		*Azolla filiculoides*	N

[a] Records from C. E. Delchamps in part.

It is remarkable that many naturalized ferns seem now to be fully "at home" in their newly adopted countries. In Hawaii particularly certain introduced species are spreading well into the native forest, especially along the foot trails, and some appear as if they were native (Wagner, 1950). To analyze the phytogeography of Hawaiian pteridophytes it is essential that we recognize which species are adventive through man's commerce and which indigenous. Failure to do so has given strange results: For example, MacCaughey (1918) listed six species as native (including one he called "endemic"!) which were actually brought in by man.

Although ferns and other pteridophytes have not been especially popular garden plants in temperate zones, they flourish in tropical plantings. Greenhouse gardeners are familiar with the experience of receiving specimens of some

TABLE 3. Considerations to determine whether disjunctive populations arose by (A) natural means or by (B) actions of man.

STANDPOINT	A. NATURAL	B. ARTIFICIAL
1. Documentation	Data confirmed and dependable	Data unconfirmable and probably erroneous
2. Transport	Unlikely to be carried by man	Likely to be carried by man
3. Flora	Area in question poorly known	Area in question well known
4. Prominence	Plant easily overlooked or confused	Plant difficult to overlook or confuse
5. Abundance	Plants numerous and in more than one colony	Plants solitary or in only one colony
6. Taxonomy	Population showing divergence	Population showing no divergence
7. Remoteness	Disjunction only a short distance	Disjunction over a long distance
8. Dispersal	Propagules capable of wide dispersal	Propagules incapable of wide dispersal
9. Pattern	Distribution pattern fits in with other, similar ones	Distribution pattern entirely peculiar
10. Habitat	Physical environment typical for taxon	Physical environment atypical
11. Associates	Adjacent species native ones	Adjacent species adventive exotic ones
12. Genetics	Reproductively self-compatible or apomictic	Reproductively self-incompatible and sexual

rare orchid or exotic gesneriad, for example, and losing the seedplant only to have it replaced by a foreign fern arising from spores in the soil. Tropical situations are probably more conducive to artificial introductions than temperate. However, in northern United States and southern Canada the Ostrich fern, *Matteuccia*, is the most popular garden fern. I wonder how many of the presumed "native" populations of Ostrich fern are actually escapes from cultivation, from either broken rhizome fragments or wind-blown spores of nearby plantings. Even some of the disjunctions listed in Table 1 may actually have resulted from man's activities.

In this connection, Fosberg (1967) repeats a wonderful story of a disjunct population of an Asiatic water lily found in a lake in Idaho: "It was assumed that here was a remarkable instance of a wide disjunction in range until someone pointed out that some years earlier there had been a Chinese laundry on the shore of this lake." What tests can we apply to evaluate whether a given disjunction was the result of artificial introduction or not? In Table 3 I have listed a number of considerations that must be applied in each case. Even mere carelessness or inadvertent error in documentation (improper labeling especially) can lead to statements of range disjunctions that never existed and create serious problems in phytogeography. The data in herbarium or publication may be erroneous but nevertheless perpetuated in the literature of botany forever. In Michigan, for example, several reports of Oliver A. Farwell are under question, these involving very large disjunctions in the Keweenaw Peninsula.

Our knowledge of disjunctions is going to be more and more concerned with artificial introductions with increasing commerce of the future. Table 3 can be used as a sort of "Index of Autochthonism" for the expanding problems of artificial disjunction in the study of plant distribution. As Fosberg (1967) points out, however, "it is frequently difficult to prove conclusively that a species was brought by man in the absence of documentary evidence directly involving the introduction."

Intrinsic Factors Bearing Upon Pteridophyte Disjunctions

Thus far we have considered mainly extrinsic factors bearing upon disjunctions. Geological history and floristic changes account for some patterns; climatic conditions for others; and human intervention for others. Prevailing winds may have produced the outliers of taxa with primarily western metropolises. Cold temperate conditions may have influenced primarily tropical rainforest species to change from the dominantly sporophytic expression of the metropolis to the dominantly gametophytic expression of the northern outposts. What of intrinsic factors such as chemical differentiation? Chromosomes? Examples of a few of these will be enumerated below.

Chemistry. Comparison of chemical aspects of disjunct populations in pteridophytes is still in its infancy. The case of the rare "Japanese grapefern," *Botrychium ternatum*, in the region of the St. Lawrence Seaway poses a number of questions. I had interpreted plants of the outlying American populations to be the same taxonomically as those of the metropolis in Japan, China, and India (Wagner, 1959; Wherry, 1961). I am still unable to separate them morphologically. My student, David M. Smith (1967), however, has shown that the American taxon differs in presence or absence of six phenolic compounds from the Japanese. In spite of these chemical contrasts I am inclined to continue treating the American plant as only varietally distinct at best. Will we find similar chemical differentiation in such disjunctive plants as *Lycopodium lucidulum*, *Osmunda claytoniana*, and *Onoclea sensibilis*? Should we treat separated populations which are morphologically alike but chemically unlike as distinct varieties?

Cytology. In Table 1, the current knowledge of level of polyploidy is indicated for the various patterns of disjunction. Most disjunctive taxa have the same chromosome number in their outliers as in their metropolis, but our knowledge is still limited and some of the examples in Table 1 may be shown to have different polyploid levels represented. One of the best known examples of polyploid differentiation is the Hart's-tongue, *Phyllitis scolopendrium*. Its metropolis in eastern Eurasia and north Africa comprises diploids (*cf.* Tryon, 1969: map 4), but its outliers in Japan and northern North America are tetraploids. The western variety of the Oak fern, *Gymnocarpium dryopteris* var. *disjunctum* is practically indistinguishable morphologically from the eastern American plant, but the former possesses $2x = 80$, the latter $2x = 160$. The Hawaiian Palaa, *Sphenomeris chinensis* (*S. chusana* of authors) is a diploid with $n = 47$, but all those populations of this taxon so far studied in India, Ceylon, and Japan are polyploid with $n = 94$ or near that number.

There are two important facets of polyploidy to consider in relation to disjunction, namely the effect it would have on the fate of the resulting population if the arriving spore were polyploid, and what causes arriving populations to remain diploid or change to polyploid. Tryon (1970) noted that Hawaii constitutes the only notable exception to the rule that ferns, in general, do not develop endemic "species flocks" on islands. He concluded that in fern floras of oceanic islands adaptability of the genotype-phenotype of the single spore to a new environment and sensitivity to selection are characteristics that dominate success in migration and evolutionary potential under geographic isolation. Our data on Hawaii seem to fit this conclusion: the incidence of polyploidy is approximately twice as great among the non-endemic taxa as it is among the endemic (Wagner & Wagner, unpubl.). According to our present evidence of *ca.* 85 percent of the fern taxa (exclusive of Ophioglossaceae and Gleicheniaceae), over 60 per cent of the non-endemic indigenous species are polyploid (3*x*, 4*x*, 6*x*, and 8*x*), but less than 30 per cent of the endemics are polyploid. Also, not one of the members of the endemic "species flocks" in Hawaii displays polyploidy (namely *Cibotium* with 5 species, *Sadleria* with 4, *Diellia* with 5, and *Adenophorus* with 8). In contrast, however, among the solitary endemics, including some of Hawaii's most distinctive taxa, there are several (*Pteris lidgatii, Thelypteris* ("*Toppingia*") *keraudreniana*, and *Microsorium spectrum*) which are tetraploids. These may constitute last remnants of earlier "species flocks" which evolved high levels of differentiation from their ancestors and are now senescent, being represented by isolated vestigial species.

Hybridity. Seven of the disjuncts discussed in this paper are interpreted as interspecific hybrids rather than normal, divergent species. They show metropolis-to-outlier disjunctions ranging from *ca.* 200 to over 2,000 miles. The outliers may be separated from one or both presumed parents. Five of the intermediates are sexual allotetraploids, and two are "sterile" allotriploids. There is no problem of accounting for long distance disjunction in the sexual hybrids, as they can spread by spores in the same manner as normal species. Our present interpretations of their origins are as follows:

Polystichum × *scopulinum* = *P. mohrioides* × *munitum*
Dryopteris × *celsa* = *D. goldiana* × *ludoviciana*
Asplenium × *pinnatifidum* = *A. montanum* × *rhizophyllum*
Pellaea × *wrightiana* = *P. longimucronata* × *ternifolia*
Cystopteris × *tennesseensis* = *C. bulbifera* × *protrusa*

The widest transcontinental disjunction of these is shown by *Polystichum* × *scopulinum*, the outlier skipping 2,400 miles of intervening country and confined to Gaspé Co., Quebec. This hybrid is a well known western American holly fern in its extensive metropolis where it occurs in both sterile diploid and fertile tetraploid forms. It is intermediate between the two species with which it most commonly grows—the amphitropical montane *P. mohrioides* and the extremely abundant and widespread endemic North American *P. munitum*. The former, *P. mohrioides*, has apparently produced no outliers east of Washington, Oregon, and California. However, the latter, *P. munitum*, which is vastly more abundant in its metropolis, has recently had an outlier reported as far east as South Dakota.

A much greater problem lies in the explanation of disjunctions of sterile triploids. *Dryopteris filix-mas* × *marginalis*, despite its abnormal spores, forms remarkably large local populations in certain localities in its metropolis, *e.g.* Bruce

Peninsula of Ontario and a few offshore islands of Lake Superior. It normally occurs with the parents near by. *Gymnocarpium* × *heterosporum* combines the characters of *G. dryopteris* ($n = 40$, 80) and *G. robertianum* ($n = 80$). None of the populations of the intermediate Oak fern has yet been discovered with normal spores. How such plants can spread if at all we can only guess. Perhaps it is by dispersion of unreduced spores (*cf.* Morzenti, 1967).

Morphology. More or less subtle anatomical differences are likely to be found between separated populations. These differences may be sufficient to designate them as different varieties or subspecies. For example, the Asiatic counterpart of *Osmunda claytoniana* differs from its eastern American representative in its hairiness (it has been separated as "var. *vestitum.*")

A particularly interesting taxonomic-geographic situation arises when we discover a disjunction of one variety in the area of another. No better example can be found than the situation in Bracken ferns, *Pteridium aquilinum* sensu lato. Most of the so-called "varieties" are allopatric and some are widely separated from the others, such as "var. *decompositum*" in the Hawaiian islands, an obviously highly disjunctive taxon. Brackens have been lumped by many authors into one species—"the only species of the monotypic genus *Pteridium* . . . ." (Tryon, 1941). However, a real question exists here, for two of the so-called "varieties" may also grow sympatrically. In March, 1970, I observed taxon *arachnoideum* intergrowing in abundance with taxon *caudatum* over a very large area of the Blue Mountains of Jamaica. The clones of these ferns differ respectively from each other in many obvious characters and they produce mixed tangles which are almost impenetrable, but which afford an excellent opportunity to compare under like site conditions. The metropolis for *arachnoideum* is mainly South American, while that for *caudatum* is southern North America and Central America. However, both coincide over a very large area of the islands of the Caribbean and the land mass of Central America.

Significance of Disjunctions in Homosporus Pteridophytes

Do long-distance disjunctions in homosporous pteridophytes necessarily give evidence of major geological and biological events in floristic history? If the disjunctions are between large and broadly distributed populations, they may indeed be highly significant as indicators of past events and relict floras. On the contrary, where the disjunctions exist between a large population center or metropolis and one or a few widely separated small populations or outliers, the significance may be less. Perhaps some of these are actually mere casual and short-lived introductions, such as those occasionally noted, say, among the butterflies, which establish themselves in a given area for a few years only to disappear. Spores of the homosporus pteridophytes are capable of long-distance dispersal by wind (Ewan, 1945; Tryon, 1970). Even though the statistical chances of a given spore reaching a given point rapidly become smaller the farther away we go from the source point, at least some spores must be able to reach highly isolated positions—as in Hawaii where the nearest sources over perhaps millions of years have been well over 2,000 miles away. The question of whether a single spore, by itself, can initiate and establish a population now seems to be satisfactorily answered in the work of Klekowski and Baker (1966, bibliography; present symposium), who find that ferns indeed are capable of intragametophytic selfing and that thus a single spore *can* start a colony.

Many of the disjunctions cited in this paper (those marked with daggers in Table 1) may be casual introductions in fairly recent times rather than "relicts" in the sense of persistent remains of ancient floras. Stanley A. Cain (1944) wrote, "Minor discontinuities of areas probably frequently result from recent migrations, but major disjunctions seem almost exclusively to have resulted from historical causes which have produced the disjunctions, in a once more nearly continuous area, through destruction or divergent migrations caused by climatic or some other changes." However, in homosporous pteridophytes, if it is true that spores can be carried long distances and produce self-fertilizing gametophytes, then we must be cautions not to read too much into long-distance disjunctions, especially those with well marked metropolis and outliers.

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